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GENERIC RELATIONS AND SPECIATION PATTERNS IN THE CARACARAS (AVES: FALCONIDAE)

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Abstract. The caracaras are a group of American Falconidae occurring from temperate and subtropical North America southward to extreme southern South America and the Falkland Islands. The taxa of caracaras appear to be closely interrelated. It is suggested that they be classified in two genera: *Daptrius* (forest caracaras; two sympatric species), and *Polyborus* (nonforest caracaras; two species-groups: the *chimachima* and *plancus* species-groups, with two and three species, respectively). Former classification advocated the use of four genera. Speciation is long completed in *Daptrius* and in the *Polyborus chimachima* species-group. In the *Polyborus plancus* species-group, however, several phenomena are evidence of active species formation. Geographical isolates exist that are morphologically differentiated enough to be considered borderline cases between species and subspecies. Some of the cases of geographical isolation in the caracaras can be related to climatic and vegetational changes following glacial events of the Pleistocene.

INTRODUCTION

This paper constitutes the fourth of a series stemming from studies on speciation in Andean birds (see Vuilleumier, 1968, 1969, 1970).

I shall discuss, first, the generic classification of the caracaras, and secondly, the patterns of distribution, geographical variation and speciation in these birds, with particular emphasis on the Andean taxa. I shall deal either with problems not, or only little, covered by Brown and Amadon (1968) in their recent book, or

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with controversial issues, especially when my own conclusions differ from theirs.

The data were obtained from examination of about 250 skins and some skeletons; and from field studies on the habitat preferences, general behavior, and distribution of five taxa of caracaras made over a period totaling thirteen months during trips to South America in 1964, 1965, and 1967-68.

THE CARACARAS

The 7 to 10 or 11 species of caracaras can be distinguished from other Falconidae more by their vulture-like external morphological characters and associated scavenging habits, than by clear-cut anatomical characters (Friedmann, 1950: 719). They differ from true falcons, however, in their habit of building their own nest, as pointed out by Brown and Amadon (1968: 23, 104). The problem of whether the caracaras should be accorded taxonomic rank within the Falconidae, and if so, which one (e.g., subfamily, tribe), will not be discussed here.

The species of caracaras have traditionally been placed in four genera (see, e.g., Peters, 1931; Hellmayr and Conover, 1949; Friedmann, 1950; de Schauensee, 1966; Brown and Amadon, 1968): *Daptrius* Vieillot, 1816, with two species; *Milvago* Spix, 1824, with two species; *Phalcoboenus* d'Orbigny, 1834, with two to four species; and *Polyborus* Vieillot, 1816, with one to three species. (The long controversy over the names *Polyborus* versus *Caracara* Merrem, 1826, was resolved by Amadon (1954), who showed that "Vieillot's diagnosis of *Polyborus* applies to the Caracaras," so that "the diagnosis sustains the name." *Caracara* must, therefore, go into synonymy, and the issue can be considered closed.)

As a group, the caracaras are distributed from temperate North America southward to Central and South America, ranging as far south as the Falklands and the islands off Tierra del Fuego. Several species have very broad ranges, especially *Polyborus plancus,* the distribution of which encompasses almost that of the entire group. Other species are, on the contrary, quite localized geographically. For example, the extinct *Polyborus lutosus* occurred only on Guadalupe Island off Baja California, and the living *Phalcoboenus australis* breeds on a handful of small islands off the southern coast of Tierra del Fuego and on the Falklands.

Correlated with the broad distribution of the caracaras is their ecological diversity. As a group, these birds inhabit most vegetation formations found in their geographical range, from desert scrub to tropical lowland wet forest, and including the highest zones of Andean vegetation. About the only major type of vegetation not favored by caracaras is montane tropical wet forest (or cloud forest).

All the taxa of caracaras are scavengers, but should perhaps be viewed as omnivorous, since their diet also includes live prey (vertebrates and invertebrates) and vegetal matter (see, e.g., Hudson, 1920: 62-88; Wetmore, 1926: 92-96; Haverschmidt, 1962: 157-158; Friedmann, 1927: 157; Friedmann and Smith, 1950: 450-451, and 1955: 486-487; Brown and Amadon, 1968). Among the most notable food specializations of the caracaras is the habit of *Polyborus plancus* of attacking domestic animals the size of sheep (Johnson, 1965: 263), and the marked predilection shown by *Daptrius americanus* for colonial wasps (Skutch, 1959).

Most caracaras are social, at least during the nonbreeding season, and form intraspecific flocks that appear to be feeding associations. The larger-sized species may form smaller flocks than the smaller ones. Thus the largest flock of the osprey-sized *Polyborus plancus* I have observed comprised about 15 birds, while I have often seen much larger flocks of the kestrel-sized *Milvago chimango.* The intraspecific gregariousness of some of the smaller species may also extend to the breeding season. Drury (personal communication) observed a colony of *Milvago chimango* where the nests were only about 30 feet (ten meters) apart. The caracaras also form associations with vertebrates other than birds. In Patagonia, *Milvago chimango* flocks are frequent near cattle and horses; I even saw one bird sitting on the flank of a lying horse, pecking from time to time at the skin, perhaps to eat ticks. Hudson (1920: 70) mentioned that *M. chimango* "follows the plough," thus playing the part of gulls (*Larus*) elsewhere. The habit of following moving vehicles from which scraps of food can be collected has been observed in *Phalcoboenus megalopterus* along the Yungas Road in La Paz, Bolivia (Niethammer, 1953: 265; personal observation), and in *Polyborus plancus* along a railroad in the Bolivian Chaco (Eisentraut, 1935: 391). The gregarious behavior exhibited by the caracaras may be correlated to a large extent with their scavenging habits, yet, from my own observations, I would judge their behavior to be much more plastic and diverse than that of other scavengers such as Old World or New World vultures (Cathartidae and Aegypiinae, respectively).

ANALYSIS OF SOME CHARACTERS OF THE CARACARAS

Size

The caracaras vary considerably in size, as several authors (Friedmann, 1950; Brown and Amadon, 1968) have already pointed out. This variation is obvious if wing length, in the absence of data on weights, is used as an indicator of overall body size (Table 1). Taxonomists have often been bothered by size differences between species, and have been reluctant to place in the same genus closely related species which differed conspicuously in size but in few, or no. other characters. This attitude might have been prevalent among the ornithologists who worked with caracaras, because the two smallest species belong in the genus *Milvago* and the largest species in *Phalcoboenus* and *Polyborus*. Yet the two species of *Daptrius* bridge the gap between these extremes. I therefore believe that size should not be given undue weight in the supraspecific classification of the caracaras. In other Falconidae, notably in the genus *Falco,* similarly large size differences between species have not prevented their inclusion in the same genus.

Proportions

In a number of bird taxa, a proportionately short tarsus is correlated with arboreal habits, and a long tarsus with more terrestrial habits. Most species of caracaras are both arboreal and terrestrial, but some definite trends toward one or the other of these habits exist, especially in regard to feeding habits. Thus *Polyborus* and *Milvago* are often seen perched on trees, and they breed in trees, but they do a lot, perhaps most, of their foraging for food on the ground. The species of *Phalcoboenus* (with the possible exception of *P. albogularis*) seem to forage entirely on the ground, and breed in cliffs and rocky slopes; they do on occasion perch on buildings. The species of *Daptrius* seem at variance with the other three genera because they do some, perhaps even a substantial, portion of their foraging for food in trees.

From this summary one would thus expect the species of *Daptrius,* which are more arboreal than the other caracaras, to have proportionately shorter tarsi than other species. Figure 1 shows a

TABLE 1

Variation of some characters among the caracaras

Taxon	*Wing length (mm)*	*Adult color*	*Immature color like adult*	*Facial skin naked (color)*	*Nostril shape*	*Habitat*
ater	294-317 (304.6) (N = 8)	black & white	no (brownish)	yes (yellow-red)	rounded	forest
americanus	327-406 (362.5) (N = 36)	black & white	yes	yes (vermilion)	rounded	forest
chimachima	255-305 (282.9) (N = 40)	brown & whitish	no (brownish)	yes (yellowish)	rounded	open woodland
chimango	276-305 (290.0) (N = 11)	brown	yes	no	rounded	open woodland
plancus	356-451 (394.6) (N = 66)	brown & white	no (brownish)	yes (yellow-red)	bean-shaped	open scrub to woodland
lutosus	402-421 (411.5) (N = 2)	dark brown	yes	yes (yellow)	bean-shaped	open country
australis	406-424 (411.8) (N = 5)	dark brownish black with white and cinnamon	no (dark brown)	yes (orange-yellow)	rounded	steppe
carunculatus	370-388 (378.7) (N = 3)	black & white	no (brownish)	yes (orange-red)	rounded	montane steppe
megalopterus	358-403 (382.5) (N = 17)	black & white	no (brownish)	yes (orange-red)	rounded	montane steppe
albogularis	357-392 (371.8) (N = 6)	black & white	no (brownish)	yes (yellow-orange)	rounded	forest (?)

scatter diagram of tarsus length plotted against wing length (representing body size in the absence of weight data) in the caracaras. The two species of *Milvago,* although overlapping considerably in wing length, show little overlap in tarsus length. The southern species, *M. chimango,* is decidedly longer-legged than the northern one, *M. chimachima.* This difference, especially in regard to the zone of sympatry of the two species, is discussed again below in the section on speciation in these birds. *Daptrius ater* has somewhat longer wings than either species of *Milvago,* but its tarsal measurements overlap fully with those of *M. chimachima.* Yet *D. ater* would seem more arboreal than *M. chimachima.* The arboreal *Daptrius americanus* overlaps with the more terrestrial *Phalcoboenus megalopterus, P. albogularis,* and *Polyborus plancus* in wing length, but has a much smaller tarsus. In this case the difference in tarsus size appears to correspond to a difference in habits.

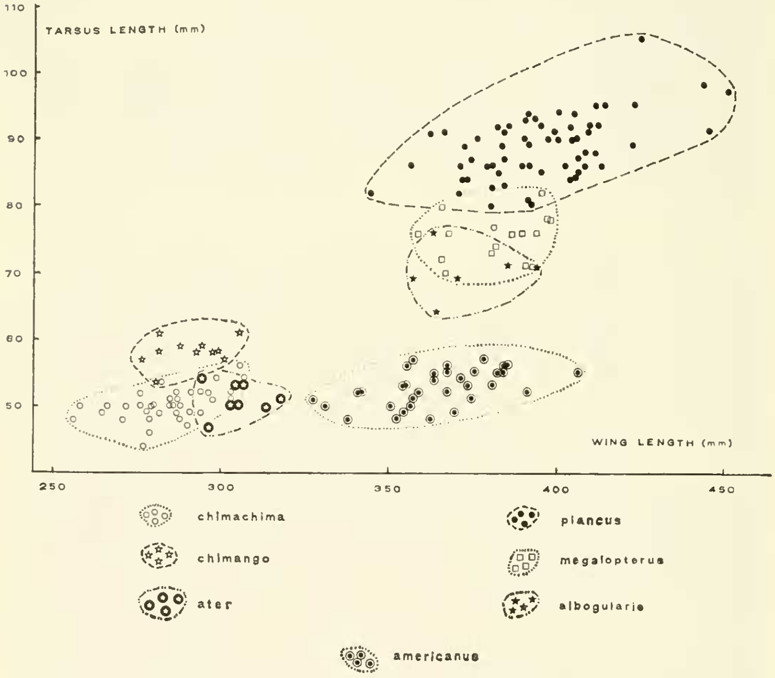

Figure 1. Tarsus length plotted against wing length in seven taxa of caracaras.

It is worthy of note that the species of *Phalcoboenus* closest to *D. americanus* in tarsus length is *P. albogularis* (see Fig. 1) said by Olrog (1948: 478; 1950: 520) to occur in forests and thus to diverge from the habitat preferred by *P. megalopterus.*

On the basis of the proportions of tarsus and wing lengths plotted on Figure 1, *Milvago chimango, M. chimachima,* and *Daptrius ater* would form one group of species closely similar to each other, overlapping greatly in both wing and tarsus length. A second such group would include *Phalcoboenus* and *Polyborus,* while *Daptrius americanus* appears clearly distinct from all other species, yet intermediate between the two groups.

Interspecific variation in tail length is summarized in Table 2. When handling skins, *Daptrius americanus* appears distinctly longer tailed than the other species of caracaras. If the tail/wing ratios, instead of the absolute tail lengths, are compared among the species of caracaras, then a smooth variation is detected, from the proportionately short-tailed *Polyborus plancus* and *Phalcoboenus megalopterus* to the long-tailed *Milvago chimachima* and *Daptrius americanus.* No groups of caracaras can be established on the basis of relative tail length.

TABLE 2

Variation in tail length, expressed in percent of wing length, among the caracaras. The taxa are ranked in order of increasing tail/wing ratio. Both sexes, and adult and subadult birds included.

Taxon	*Tail/Wing × 100*		*Sample Size*
	Range	*Mean*	
plancus	50.8-58.1	53.9	42
megalopterus	53.1-57.4	55.5	13
carunculatus	—	55.6	1
chimango	54.8-58.7	57.3	5
albogularis	54.1-64.7	58.4	5
australis	57.5-61.5	59.4	4
ater	58.4-63.5	61.1	6
lutosus	—	62.7	1
chimachima	60.9-70.2	66.2	25
americanus	62.2-74.6	68.4	36

Plumage Color and Pattern

Good descriptions of both adult and immature plumages of caracaras have been given by Friedmann (1950) and Brown and Amadon (1968), who should be consulted for full details. The main colors of adult and immature plumages are summarized in Table 1.

Adult caracaras vary from a brown, rather unpatterned plumage (such as is found in a variety of birds of prey) to a highly patterned plumage. Thus *Milvago chimango* has a brown plumage, variegated somewhat with barrings, reminiscent of the plumage of some kites of the genus *Milvus*. The plumages of both species of *Daptrius*, and of the three Andean species of *Phalcoboenus* (*carunculatus, megalopterus,* and *albogularis*) are very different from those of the other caracaras. These birds are strikingly marked with black and white patterns, and remind one of gallinaceous birds such as *Crax*.

Immature caracaras are less varied in their plumages. Most of them are brownish with patterns of barring or streaking, with the exception of the immature *Daptrius americanus*, which is like the adult. The dimorphism between immature and adult can be very well marked, as in *Phalcoboenus carunculatus, P. megalopterus,* and *P. albogularis;* or poorly marked, as in *Daptrius americanus* or *Milvago chimango;* or intermediate, as in *Polyborus plancus* and *P. lutosus*.

In spite of the variation in plumage color and pattern exhibited by the different species of caracaras, certain basic resemblances are evident in the group as a whole when adult and immature plumages are compared together. For example, the immatures of *Milvago chimachima, Phalcoboenus carunculatus, P. megalopterus, P. albogularis, Polyborus lutosus* and *P. plancus* are all very similar to one another, as they are to the adult of *Milvago chimango*. Thus, regardless of the intraspecific variability between immatures and adults on the one hand, and the interspecific variability among adults on the other, *Milvago, Phalcoboenus,* and *Polyborus* all appear to have similarities in plumage color and pattern.

In every genus except *Polyborus,* there is a dichotomy between one or more species that have different immature and adult plumages, and one or more species that have quite similar immature and adult plumages. This dichotomy is obvious in *Milvago,* with *chimango* plumages much alike, and *chimachima* unlike; in *Phalcoboenus,* with *australis* plumages much alike, and with *carunculatus-megalopterus-albogularis* plumages very different. The dichotomy is still present, but much less obvious, in *Daptrius,* with *americanus* plumages alike and *ater* plumages slightly different. Correlation between this dichotomy and patterns of geographical distribution among closely related species is not readily apparent. In *Milvago* and *Phalcoboenus,* the species which differ least in their adult and immature plumages are the two southern ones; but in *Milvago* alone, there is an important geographical overlap between *chimango* and *chimachima,* whereas there is no or only a very narrow overlap between the southern *australis* and the more northern *carunculatus-megalopterus-albogularis* complex. In *Daptrius* (dichotomy poorly marked), there is almost complete overlap between the ranges of the two species, since the range of *ater* is almost entirely contained within that of *americanus.* In *Polyborus* (no, or almost no dichotomy), *lutosus* and *plancus* are entirely allopatric. (The possible ecological significance of the immature and adult dimorphism is discussed below under habitat preferences.)

If one were to consider the immature-like plumage of some sexually mature birds as being a primitive condition, and the strikingly different plumage in other mature birds as an advanced one (i.e., secondarily developed during the evolutionary history of the caracaras), then *Polyborus* and *Daptrius* might be thought to be more primitive than the other two genera. If a brownish, barred and streaked immature plumage were considered a more primitive condition, then *Daptrius* is more advanced in this character than the three other genera, because in that genus, immatures are hardly different from adults, being also conspicuously patterned in black and white.

Naked Facial Skin

Every species in the genera *Polyborus, Phalcoboenus,* and *Daptrius* has brightly colored naked skin between the bill and the eye, and often around the eye or even the throat. In the genus *Milvago,* only *M. chimachima* has naked facial skin; *M. chimango* has a fully feathered head. The area of unfeathered skin varies from species to species among those that have naked facial skin. In the species of *Phalcoboenus,* this variation is geographical. In *Phalcoboenus carunculatus* (Colombia and Ecuador), the surface of facial skin is extensive, and the throat is even adorned by fleshy wattles. In

P. megalopterus (Peru, Bolivia, and northern Chile-Argentina), only the lores are unfeathered, while the throat is largely feathered. In *P. albogularis* (Patagonia), the extent of bare loral skin is smaller than in *megalopterus*. Finally, in *P. australis* (southernmost islands of South America), the facial skin is almost entirely feathered, but there are wattles on the breast instead. The difference between *P. australis* and *P. carunculatus-megalopterus-albogularis* may be related to the fact that *australis* is sympatric with *Polyborus plancus,* a species having extensive naked facial skin, whereas the other three species of *Phalcoboenus* are the only caracaras in their respective ranges.

The naked facial skin in the caracaras varies from salmon pink to rose-red and from yellowish to bright red (see Table 1). This variation is both intra- and interspecific. I have seen the facial skin of one individual of *Polyborus plancus* change, in a few seconds, from pale yellow to salmon-pink and finally to vivid red. Such a rapid change cannot easily be ascribed to hormonal influences, but is more likely to be due to a sudden flush of blood to the superficial vessels of the skin. Brown and Amadon (1968: 738) mention a reverse change in *P. plancus*: "bare facial skin carmine red, changing to yellow when excited."

The variation in facial skin color in the caracaras (Table 1) seems too extensive within species, and too restricted between species (differences between, say, yellow and orange, or orange and red seem relatively slight) to be important as a species-specific means of recognition. Presence or absence, together with color and area of unfeathered skin might, however, play such a role among true sympatric species, e.g., *Phalcoboenus australis* and *Polyborus plancus* already cited, or *Milvago chimango* and *M. chimachima.*

Nostril Shape

I have examined skulls of *Polyborus plancus* (several specimens), *Phalcoboenus australis* (4), *Daptrius* sp. (1), and *Milvago* sp. (3). *Polyborus plancus* has slanted, elongated nostrils (bean-shaped), while *Phalcoboenus australis, Daptrius* sp., and *Milvago* sp. all have rounded nostrils. This difference is also visible on the cere of study skins and seems to be confined to *Polyborus* (Table 1), since only *P. lutosus* and *P. plancus* have bean-shaped nostrils. Swann (1925: 66) and Friedmann (1950: 545-546) used this difference in nostril shape, together with other characters, as diagnostic features to key out the genera of caracaras. I do not know what the biological significance of this difference may be.

Habitat Preferences

The preferred habitats of *Milvago, Phalcoboenus,* and *Polyborus* include a variety of nonforest types: open scrub, grassy pampas, tussock-grassland, pastures, treeless cultivated farmland, open thorny chaco, savanna woodland, and open plantations. *Phalcoboenus albogularis* may be an exception, since Olrog (1948: 478; 1950: 520) reports it as a forest bird.

Both species of *Daptrius* are inhabitants of tropical forest and contrast markedly with the other caracaras in this feature. The distribution of *ater* and *americanus* corresponds to the distribution of wet lowland rain forest in Central and South America, but the actual preference of these species seems to be less for the forest interior than for more open situations within or along the forest: river banks, small clearings, secondary growth, mangroves, and tree-tops. The plumage pattern of both species of *Daptrius,* especially *D. americanus,* is most similar to that of adults of *Phalcoboenus carunculatus* and *P. megalopterus,* which inhabit high Andean steppes, an environment that differs in every respect from that of *Daptrius.* This basic morphological similarity among taxa of widely distinct ecological preferences seems to be more easily understandable on an hypothesis of close relationship than on one of convergent evolution. The fact that the species of *Phalcoboenus* mentioned above have a very different immature plumage, while those of *Daptrius* are far less dimorphic between adult and immature, might be a correlate of environmental differences between the two genera. In the open habitats of the high Andes there is never more than one species of caracara at any one locality (diversity = 1). Because congeneric competitors are absent, the sharp dimorphism between adults and immatures of *Phalcoboenus* may consequently reflect the results of slightly relaxed selective pressures. In the tropical lowland forests, however, there are two sympatric species of caracaras (diversity = 2), so that selection through interspecific competition might possibly limit the range of intraspecific variability, thus resulting in the evolution of similarity (monomorphism) between immatures and adults of *Daptrius.* The difference in size (character divergence) between the two species of *Daptrius,* which are sympatric, may be relevant here. Being so different from each other (no overlap in range of wing lengths), they should compete very little for food (see Schoener, 1965). The interspecific difference in size, together with the lack of dimorphism between age categories in *Daptrius,* may be roughly equivalent ecologically to the striking dimorphism within high Andean *Phalcoboenus,* which do not have any sympatric congeners. In *Milvago,* where the two species are largely allopatric, one observes a considerable overlap in wing lengths between the two, but one of the species is conspicuously dimorphic (*chimachima*), whereas the other is not. Therefore, the situation in *Milvago* appears intermediate to that in both *Daptrius* and *Phalcoboenus.* I believe this intermediacy is also found in the habitats occupied by *Milvago* (such as open woodland, savannas) that are more or less intermediate between lowland wet forest (occupied by *Daptrius*) and barren high Andean steppes (occupied by *Phalcoboenus*).

Summary of Character Analysis

If the characters discussed above are examined separately, the variation among some of them shows the following possible grouping within the caracaras. (a) *Polyborus* is distinct in nostril shape from the other genera. (b) *Daptrius* and *Phalcoboenus* are closer to each other than to other genera since both have a strikingly patterned black and white adult plumage. (c) The immature plumages of *Milvago, Phalcoboenus* and *Polyborus* appear extremely similar to one another, and differ, as a group, from those of *Daptrius.* If both adult and immature plumages are used, together with habitat preferences, the two species of *Daptrius* appear to stand out against most other species. First, the immature plumage of *Daptrius,* when distinct from that of the adult (as in *D. ater*), is quite different from the brownish, streaked or barred immature plumage of all other species except *Phalcoboenus australis.* Secondly, the forest habitat of the species of *Daptrius* differs from the nonforest habitats of the species in the other genera, with the possible exception of *Phalcoboenus albogularis.* (The remaining characters [naked facial skin and size] seem of little or no use in establishing groups within the caracaras.)

I can only conclude from this analysis that all caracaras appear to be closely interrelated, but that *Daptrius* is less similar to the other three genera than these are to each other.

CLASSIFICATION

The splitting of the caracaras into four genera, endorsed by most taxonomists, does not seem to reflect properly the close relationships of these birds. Since the lumping of all caracaras into a single genus may be going somewhat too far in the opposite direction, I suggest here a third possibility, which is to put the caracaras inhabiting nonforest habitats in a single genus (*Polyborus,* including *Milvago* and *Phalcoboenus*) and to keep the forest caracaras in a second genus (*Daptrius*). Further subdivisions within the nonforest caracaras can be made by using species-groups and superspecies, which do not burden the nomenclature with additional names (as pointed out by Cain, 1954), yet permit a finer hierarchy between the genus and species levels.

I present below a classification outline of the caracaras, including species-groups and superspecies. Each species-group represents a former genus. The grouping of some species in a superspecies (included in braces) is given here in anticipation of the discussion on speciation in the next section of this paper. The sequence of taxa in this list is arbitrary, and does not pretend to suggest that some taxa are more primitive than others, since such decisions would be guess work.

Genus *Daptrius* Vieillot, 1816 (forest caracaras)
    D. ater Vieillot, 1816
    D. americanus (Boddaert, 1783)

Genus *Polyborus* Vieillot, 1816 (nonforest caracaras)

1. *chimachima* species-group
    - *P. chimachima* Vieillot, 1816
    - *P. chimango* Vieillot, 1816
2. *plancus* species-group
    - *P. plancus* (Miller, 1777) (includes *lutosus* Ridgway, 1876, considered by some authors as a separate species)

    australis superspecies
    - { *P. australis* (Gmelin, 1788)
    - { *P. megalopterus* (Meyen, 1834) (includes *carunculatus* (Des Murs, 1853), and *albogularis* Gould, 1837, considered by some authors as two separate species)

VARIATION AND SPECIATION IN *DAPTRIUS*

Of the two species of *Daptrius,* only *D. americanus* shows geographical variation. This variation seems to be a cline of diminishing size, as measured by wing length, from Guatemala southward through Central America to South America. According to Brown and Amadon (1968), the populations from "southern Brazil" may show an increase in wing length over those from farther north in South America. This increase is in fact quite sharp, and is illustrated by Figure 2. The disjunction may reflect absence of gene flow between birds from the Amazon Valley and those from the uplands of Brazil. The birds living in the coastal forests of southern Brazil and in the gallery forests of the Paraná-Paraguay drainage system of south-central Brazil may be ecologically isolated from birds living in forests of the Amazon Valley by parts of the central Brazilian plateau, which are covered by extensive open savannas and campos.

Any inferences that might be drawn about the possible evolutionary history of this genus are prevented by the considerable sympatry between *ater* and *americanus* (see map 76 in Brown and Amadon, 1968).

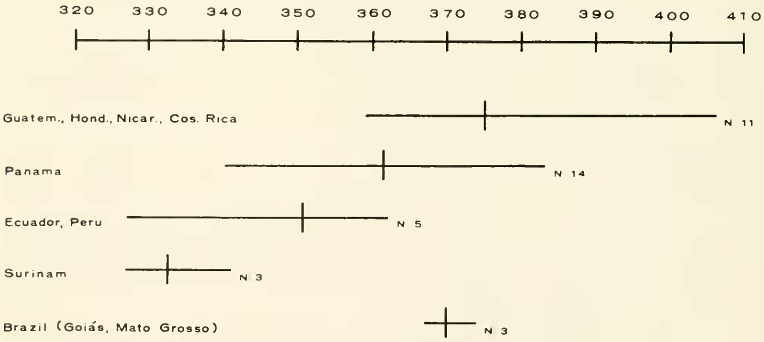

Figure 2. Geographical variation of wing length in *Daptrius americanus.* Measurements are in millimeters. Horizontal bars: range of measurements; vertical bars: means.

VARIATION AND SPECIATION IN *POLYBORUS*

1. The *chimachima* Species-Group

The two species of this group, which constitute the former genus *Milvago,* are largely allopatric. *Polyborus chimachima* occurs in southern Central America (Costa Rica and Panama) and in South America from Colombia and Venezuela in the north to northern Argentina in the south, and *P. chimango* from northern Argentina southward to southernmost South America. They are sympatric, however, over a relatively broad zone, including Rio Grande do Sul in southern Brazil, parts of northern Argentina, Uruguay, and Paraguay, and southern Bolivia westward to the foothills of the Andes.

Polyborus chimachima shows color and size variation. Tail and culmen length appear to vary clinally, and to increase from south to north, whereas the reverse seems to be true of wing length (see Fig. 3).

Polyborus chimango shows geographical variation that seems to conform to eco-geographical rules, since the southernmost birds are the largest (Bergmann's rule), and the birds occurring along the wet, forested Andean slopes are darker than those living in the drier, grassy and shrubby plains of central Argentina (Gloger's rule).

Geographical variation in *P. chimango* has been recognized taxonomically by the naming of three subspecies. Two of them, *temucoensis* (Andean slopes birds) and *chimango* (open plains birds) intergrade broadly. The third subspecies, *fuegiensis,* seems restricted to the island of Tierra del Fuego, but is probably merely the southward end of a north to south cline of increasing size. Interestingly, the southern populations, from Tierra del Fuego and the mainland of southern Patagonia, appear to leave their breeding grounds to migrate northward as far as northern Argentina (Olrog, 1962: 112-113) in the southern hemisphere winter.

Although *P. chimachima* and *P. chimango* are undoubtedly very close relatives, they have diverged morphologically rather considerably. One of the differences has been mentioned earlier: the immature plumage of *chimango* is very similar to that of the adults, whereas the immature *chimachima* is quite unlike the adult. Another difference between the two species may be ecological. As I

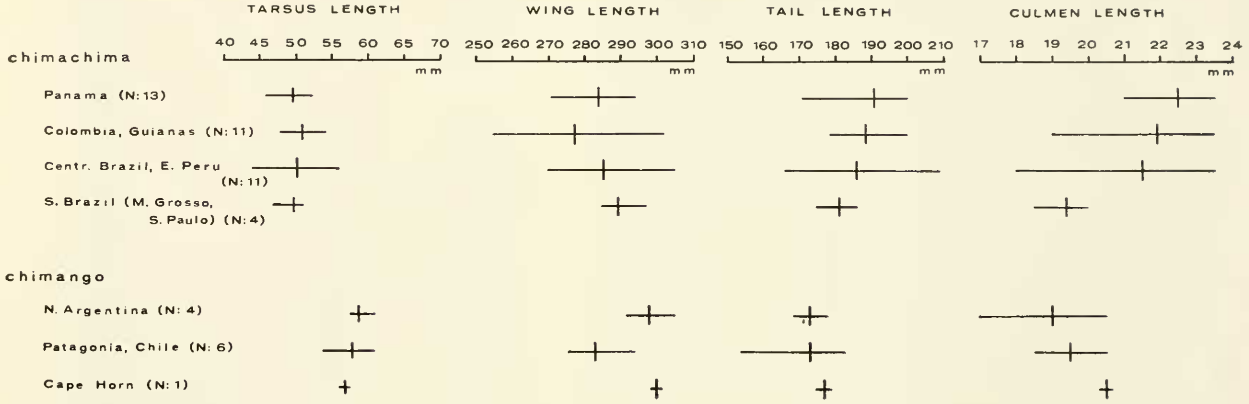

Figure 3. Geographical variations of tarsus, wing, tail, and culmen lengths in *Polyborus chimachima* and *P. chimango*. Horizontal bars: range of measurements; vertical bars: means.

judge from personal observations and literature records, *P. chimachima* may generally prefer somewhat denser, more wooded, habitats than *P. chimango,* but no study of a possible habitat segregation has been undertaken in the area of sympatry. If tarsus length reflects whether a bird is more or less arboreal, then variation between *P. chimachima* and *P. chimango* in this character is instructive. That *P. chimachima* populations have shorter tarsi than those of *P. chimango* (see Fig. 3) suggests that the latter may be less arboreal than the former. Whether this difference is true character divergence should be examined carefully.

Brown and Amadon (1968: 739) say that the two species "may be regarded as a super-species." Even if a broad superspecies concept is embraced, it seems to me that the zone of overlap, considered together with the morphological differentiation between *chimachima* and *chimango,* clearly suggests that these two taxa are past the species borderline, and that application of the superspecies concept to their case may no longer be correct. As far as I know, hybridization does not take place between the two species where they are sympatric; a field study of the pair in their overlap zone would nevertheless be rewarding.

It seems most likely that the pair of species *chimachima* and *chimango* has originated by a straightforward process of splitting of one ancestral population into two. Yet secondary sympatry is too extensive to permit more speculation about the original isolation.

2. The *plancus* Species-Group

This group consists of *P. plancus* and the *P. australis* superspecies. The birds of this group are medium to large, and have brownish immature plumage with dark streaking and/or barring. The *P. plancus* species-group includes both the former genera *Polyborus* and *Phalcoboenus.* Brown and Amadon (1968: 730) remarked that *"Phalcoboenus australis* is in all respects intermediate" between *Polyborus* and *Phalcoboenus,* yet they kept the two genera distinct.

P. plancus is essentially a lowland species, while the members of the *P. australis* superspecies occur mostly in the Andes, in some localities at high altitudes. Where *plancus* meets members of the *australis* superspecies, as on the Falkland Islands and on islands off Tierra del Fuego, the two may live in habitat co-occupancy, but their ecological relationships have not been studied. In any event, sympathy in the *P. plancus* species-group is very limited and geographically peripheral.

Polyborus plancus

Polyborus plancus has a broad distribution from the southern United States and Mexico to Tierra del Fuego and the Falkland Islands and exhibits extensive geographical variation. The birds from Florida, isolated from the remainder of the mainland North American birds, are closer geographically and morphologically to the Cuban ones (both are included in the subspecies *auduboni*). The birds of the population living on the Tres Marías Islands off western Mexico (subspecies *pallidus*) are morphologically differentiated from the nearest mainland populations (for a discussion of the characters of *pallidus*, see Grant, 1965: 12-14). The continental population living from eastern Panama southward to northwestern Peru near the Upper Marañon and Amazon Rivers (subspecies *cheriway*) are well marked. There is intergradation between *cheriway* and southern South American birds (subspecies *plancus*) in Brazil (see Hellmayr and Conover, 1949: 283-284).

The extinct *Polyborus lutosus* lived on Guadalupe Island (see e.g., Abbott, 1933; Greenway, 1958). The adults looked very similar to *plancus*, but white was replaced by brown, and there was no black on the abdomen; the immature was brown and streaked. This insular population was certainly well marked; it is considered here as having been a strong subspecies of *plancus*. Brown and Amadon (1968: 736) maintained *lutosus* as a separate species.

The *australis* Superspecies

The four nominal species (the former genus *Phalcoboenus*) included in this superspecies are Andean and Patagonian in distribution (Fig. 4). One of the species, *australis*, occurs only on islands off southern South America. The three others, *carunculatus, megalopterus*, and *albogularis*, occur along the Andean cordillera, from Colombia to Tierra del Fuego.

Polyborus australis is larger than the three other species, but resembles them in several other respects. The pattern of breast and abdominal streaks in the adults is especially reminiscent of the geographically distant *carunculatus*. *P. australis* breeds on the Falklands, where, according to Cawkell and Hamilton (1961), its numbers have decreased in the recent past. It also breeds on several islands off Tierra del Fuego (Staten and Navarino), and on islands of the Cape Horn Archipelago (for example, Grevy, Bayly,

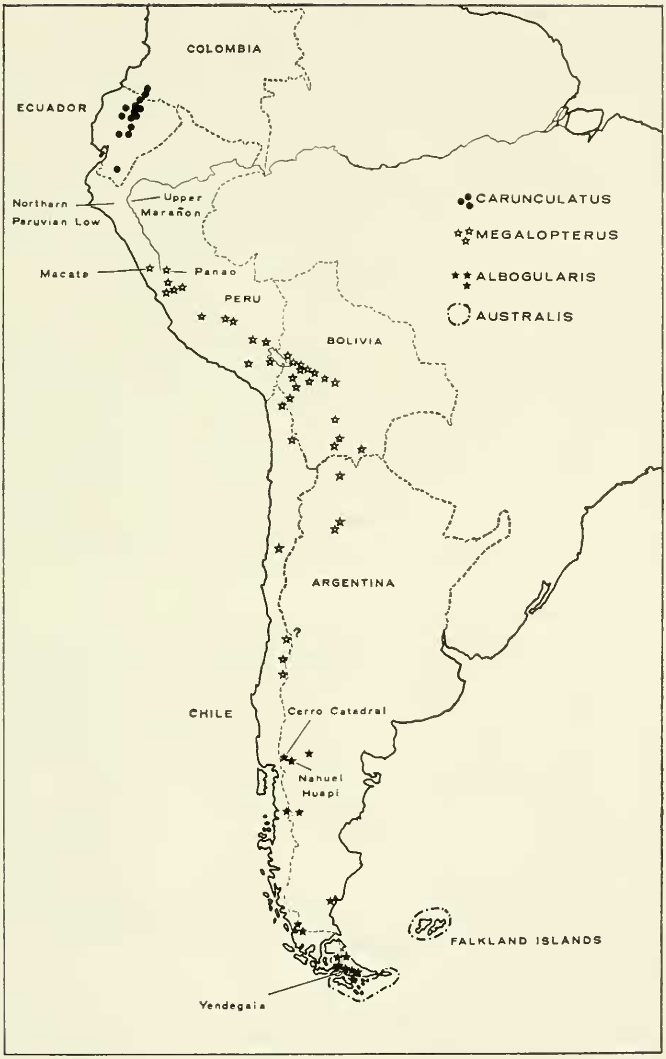

Figure 4. Geographical distribution of the *Polyborus australis* superspecies. A question mark represents the alleged occurrence of *albogularis* at Puente del Inca, Mendoza (see Hellmayr and Conover, 1949: 277-278). Labeled localities are identified in the text.

Freycinet, Hershel: Olrog: 1950: 520). Reynolds (1932) observed one *P. australis* on Woodcock Island in the Beagle Channel, and Olrog (1948: 478) saw it at Yendegaia, along the southern coast of Tierra del Fuego, where he also collected *P. megalopterus albogularis* (see Fig. 4). This observation (not mentioned by Brown and Amadon, 1968: 731) implies that *P. australis* and *P. megalopterus albogularis* are narrowly sympatric on the main island of Tierra del Fuego, but this suggestion needs careful checking in the field. *P. australis* is sympatric with *P. plancus* on some islands off Tierra del Fuego and the Falklands.

Polyborus carunculatus, megalopterus, and *albogularis* are here treated as three subspecies of a single species, as previously advocated by Hellmayr and Conover (1949: 276-277), and adopted later by some students of South American birds (e.g., Olrog, 1963; Koepcke, 1964; and Johnson, 1965). (The name *megalopterus* Meyen, 1834, has priority over *albogularis* Gould, 1837, and should be used as the specific name, *contra* Hellmayr and Conover, 1949.) Other authors, however, have maintained the three taxa as separate species (e.g., Amadon, 1964: 14; de Schauensee, 1966; Brown and Amadon, 1968).

The divergence of opinion about the taxonomic status of these three taxa has hinged on two things: first, the striking interspecific adult plumage color differences, and secondly, the allopatry of the taxa. A third factor, namely the absence of intermediate specimens between any two of these forms, has been invoked by some authors to justify their treating the three as species. Brown and Amadon (1968: 371), for instance, stated: "the two [taxa] that are the most similar, *albogularis* and *megalopterus,* are not known to intergrade rather [sic] there seems to be a slight gap between their ranges, suggesting friction." A few specimens, however, do seem to be intermediate between *carunculatus* and *megalopterus* on the one hand, and between *megalopterus* and *albogularis* on the other, as discussed below.

The characters that vary from one to the other of the three taxa, *carunculatus, megalopterus* and *albogularis,* are: the amount of white at the tip of the primaries, the degree of curliness of the crest feathers, the extent of bare skin on the throat, and the coloration of the underparts. The two northern taxa, *carunculatus* and *megalopterus,* live in high Andean grassland and scrub above the timber line, at altitudes usually higher than 3000–3500 meters. Both of these forms are common birds where they live, and can be seen daily in small groups or singly (personal observation). The populations of *carunculatus* are geographically isolated from those of *megalopterus* by a hiatus that includes the low Andes of northern Peru, the depression of the Upper Marañon Valley and other valleys in northern Peru (see Fig. 4). Birds north of this gap (*carunculatus*) have the throat and breast black with white longitudinal streaks or spots, and the abdomen white. South of the gap, birds (*megalopterus*) have throat and breast black without white spotting or streaking, and a white abdomen.

These morphological differences, considered in the light of the ecological barrier lying between the two taxa, might be interpreted as reflecting a period of geographical isolation during which differential selection acted on populations cut off from free gene flow. Absence of gene flow, however, seems surprising in view of the good flying abilities and the relative abundance of birds of this group. It is therefore noteworthy that Zimmer (1930: 248) found three adult males of *megalopterus* from Peru, all showing "an interesting progression in the direction of *carunculatus*." Two of the three specimens (from Macate, Department Ancash, and Panao, Department Huánuco, see Fig. 4), have small, pale or whitish spots on the lower breast; the third specimen (from Junín, farther south) lacks breast spots. Zimmer's description of the three birds should be consulted for additional details.

These data seem to indicate that gene flow is indeed possible between Ecuadorian *carunculatus* and Peruvian *megalopterus*. Further intensive collecting of these birds in northern Peru is badly needed. The total number of specimens of either *carunculatus* or *megalopterus* from areas close to the barrier of northern Peru is low, so hybrid specimens might appear to be much rarer than they really are.

What about the situation between *megalopterus* and *albogularis?* The northern *megalopterus* is a common bird in the high Andean scrub vegetation of the Argentine-Chilean cordilleras. The southern *albogularis* seems to occur in *Nothofagus* forests rather than open vegetation types (see Olrog, 1948: 478; 1950: 520; Philippi *et al.*, 1954: 39). There seems to be a distributional hiatus (see Fig. 4) between the northernmost records of *albogularis* (in Neuquén, *fide* Olrog, 1963: 116) and the southernmost ones of *megalopterus* (in Talca, *fide* Johnson, 1965: 265). We do not know, however, whether this gap is real or not, because of the general scarcity of collections made in the "hiatus" area. In any event, what is real is the fact that no ecological barrier interrupts the distribution of *megalopterus* and that of *albogularis* in the way the northern Peruvian low does between *megalopterus* and *caruncculatus*. The situation seems therefore more complex ecologically, and deserves field study.

From these considerations, contact should be possible between *megalopterus* and *albogularis,* and if they are not reproductively isolated, gene flow should occur between them. In February, 1965, at 1950 m on Cerro Catedral, near Nahuel Huapi, Río Negro, Argentina (see Fig. 4), I observed two adult *Polyborus* that were attracted by a small garbage dump near the Refugio Lynch. One of them had the throat and breast black, in contrast with the white of the abdomen (*megalopterus*-like phenotype). The second had both a white throat and breast, with only the sides of the breast black, not forming a black pectoral band (*albogularis*-like phenotype). This observation might have been of a mixed pair, but unfortunately the birds could not be collected.

The possibility of mixed pairs and of offspring from them, seems to be shown by two adult birds that exhibit what appears to be intermediacy between *megalopterus* and *albogularis*. One of these birds, an adult male taken in February, 1896, in Chubut, southern Argentina, was described by Scott (1910) as *Ibycter circumcinctus*. The underparts of this specimen are as follows: the throat is white, followed by "a band of black below the throat patch more or less variegated by white on some of the feathers; this band is about an inch in width; lower part of the under neck pure white, the black of the sides of the neck confining the white of this region to a narrow area, widening into the pure white of the breast." This bird appears to be like a specimen of *albogularis* with a narrow black breast band. The second of these birds, an adult male from Nahuel Huapi (see Fig. 4), is mentioned by Hellmayr and Conover (1949: 277). This specimen (British Museum 99.1.27.229) has a distinct, interrupted breastband.

The same conclusion seems, therefore, to follow from these scanty data as from those on *caruncculatus* and *megalopterus*: contact between *megalopterus* and *albogularis* seems a reality since at least two specimens are somewhat intermediate between the two taxa, and since birds from the two phenotypes were sighted together. Amadon, however, speaking of Scott's "*circumcinctus,*" said that it "may be a mutant rather than a true genetic intergrade" (1964: 15). This hypothesis seems unlikely to me. Since specimens of *albogularis* are relatively rare in museums, the two birds with a black pectoral band represent a relatively high frequency of the black-banded phenotype, perhaps as many as 1 in 10 or 1 in 15—a number too high to be accounted for solely on the basis of recurrent mutation. A third possible interpretation would be that there is a polymorphism involving breast color. If this were true, then obviously *megalopterus* and *albogularis* should be considered members of the same species.

For the time being, I believe the best interpretation of the situation in this complex to be that the three taxa, although clearly differentiated morphologically as adults, have not achieved complete reproductive isolation, so that when two of them come in contact, whether across a barrier (*carunculatus* with *megalopterus*) or not (*megalopterus* and *albogularis*), they produce hybrids. The taxonomic solution I propose in this paper is to consider all three taxa conspecific, although I realize that this lumping may be a little premature in view of the paucity of data. If additional study should reveal that hybridization is very limited, even though there may be plenty of opportunity for it to take place, then it would be justified to maintain the three taxa as species, although it would be necessary to emphasize that they are really semispecies: a truly intermediate stage in the speciation process.

DISCUSSION

The caracaras are interesting to the student of speciation, because they offer a variety of phenomena that are interpreted as intermediate in the process of species formation (see Table 3). They can be summarized as follows. In *Daptrius americanus,* the populations from southern Brazil may be geographically isolated from other populations farther north in South America. In *Polyborus plancus* can be seen phenomena of incipient speciation. Isolated populations, both insular (Tres Marías Islands, Cuba) and continental, exist, showing varying degrees of morphological differentiation. The most differentiated population (*lutosus*) was wholly insular, yet was of no evolutionary significance for further speciation since it is now extinct. The other insular populations, on the Tres Marías Islands and Cuba, are much less differentiated than *lutosus,* the Cuban one even being similar morphologically to the Florida population. On the continent, populations from northern South America (*cheriway*) are sufficiently differentiated from southern South American ones (*plancus*) for some ornithologists

TABLE 3

Stages of the speciation process in the caracaras

Species or semispecies	*Geographical variation*			*Secondary contacts*	*Members of a superspecies*	*Closest relative sympatric*
	Absent	*Clinal*	*Discontinuous (morphologically differentiated isolates)*			
Daptrius ater	+	–	–	–	–	+
Daptrius americanus	–	–	+[1]	–	–	+
Polyborus chimachima	–	+	–	–	–	+[2]
Polyborus chimango	–	+	–	–	–	+[2]
Polyborus plancus	–	–	+	+[3]	–	–
Polyborus australis	+	–	–	–	+	–
Polyborus megalopterus	–	–	+	+	+	–
Totals: 6	2	2	3	2	2	4

[1] *Daptrius americanus* has an apparently isolated population in southern Brazil

[2] *Polyborus chimachima* and *P. chimango* overlap in their distribution, yet are partially allopatric

[3] *Polyborus plancus* may exhibit secondary contact phenomena in South America

to have treated them as species. There is some evidence that (secondary?) hybridization takes place near the mouth of the Amazon where they come into contact.

The taxa of the *Polyborus australis* superspecies present another "stage" of the speciation process, in that one of the members of the superspecies, *australis,* is sufficiently distinct to be considered unhesitatingly as a species. The three remaining members, however, present interesting situations. In one instance, differentiation seems to have taken place across an ecological barrier (the low area of the northern Peruvian Andes), yet hybridization appears to occur in spite of this gap. In the second instance, no barrier is evident today, and some hybridization seems to occur. The southernmost taxon of this complex (*albogularis*) apparently meets *australis* in Tierra del Fuego.

In the *Polyborus chimachima* species-group, speciation is completed, and the two species overlap now over a considerable area, although they are allopatric over the major portions of their respective ranges. Finally, the two species of the genus *Daptrius* are so different morphologically and show so much sympatry that reconstruction of their history is impossible.

Although six of the seven species I recognize in the caracaras have extensive geographical distributions, the existing patterns of speciation, or incipient speciation, seem to indicate that multiplication of species has occurred mostly through the formation, and subsequent differentiation, of small or relatively small peripheral isolates. The present isolates of *Daptrius americanus* and *Polyborus plancus* are restricted to small areas around the periphery of the range of the species, and the geographical location of *Polyborus australis* relative to *Polyborus megalopterus* seems to suggest former peripheral isolation of the first named species. Differentiation within *P. megalopterus* does not seem to correspond as clearly to a pattern of isolation in peripheral areas, although the central populations (*megalopterus*) do have a much broader distribution than either the northern (*carunculatus*) or southern (*albogularis*) ones.

The previous summary of speciation in the caracaras shows that this process is most actively taking place along the Andes, where the various members of the *Polyborus australis* superspecies live. In the other, lowland, taxa, the speciation process is either completed (as in *Daptrius* or the *Polyborus chimachima* species-group) or is not as pronounced (*Polyborus plancus, Daptrius americanus*).

It is tempting to relate the apparently greater evolutionary activity in the Andean caracaras to the recent geological history of this cordillera. The high Andean grasslands and scrub habitats (páramo and puna) where *Polyborus megalopterus* now lives are undoubtedly the most recent environments of the Andes, and cannot be older than the latest phases of uplift, which brought the mountains to their present tremendous altitudes during the Plio-Pleistocene (see Childs and Beebe, 1963; Steinmann, 1930; Ahlfeld and Branisa, 1960; and Brüggen, 1950; for summaries of the geological development of the Andes). The differentiation within *P. megalopterus* most probably occurred during the Pleistocene glaciations, although to attempt the dating of such processes is almost complete guess work. However, if we recall that during glacial episodes, the temperature depression lowered the altitude of the upper vegetation zones, where *P. megalopterus* lives, then it becomes possible to envision the separation of a northern isolate (proto-*carunculatus*) in Ecuador at interglacial time, when the altitudinal raising of this treeless zone occurred, thus increasing the effectiveness of a natural barrier such as the Upper Marañon Valley and northern Peruvian low for birds living on either side of it. The isolation of *carunculatus* from *megalopterus,* or, rather, of proto-*carunculatus* from proto-*megalopterus,* might, then, have happened during an interglacial. It is, of course, not possible to suggest which of the several interglacial periods was responsible for such an event.

Similar glacial-interglacial oscillations may have permitted the separation of proto-*megalopterus* and proto-*australis* in extreme southern South America. During the maximum glacial, extreme southern South America was covered with an ice-sheet (Caldenius, 1932; Polanski, 1965) which probably forced Andean biota to "retreat" considerably northward. At the same time, however, the Falkland Islands were left unglaciated, and, furthermore, were of greater area than today because of a concurrent lowering in sea-level. It seems therefore possible that during the maximum glaciation the southernmost populations of the stock common to *megalopterus* and *australis* remained on a Falkland refuge, where they were geographically isolated from mainland populations by the ice barrier, added to the sea barrier. If such a separation did indeed take place during the maximum glaciation, which is attributed to the late Pleistocene (Würm or Wisconsin) (see Polanski, 1965), then the splitting of an ancestral stock into the modern *australis* (having evolved from a population in a southern insular refuge) and *megalopterus* (having remained in Andean Patagonia, but considerably farther north than its present-day southernmost limit) may have taken place as recently as 50,000 to 80,000 years ago. Of course, it is also possible that the original separation took place during an earlier, somewhat less extensive, glacial episode, but since the maximum glaciation apparently obliterated earlier remains, it is futile to speculate any further about the possible course of this event.

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